The Journal of Research on the Lepidoptera Volume 48: 13-20

ISSN 0022-4324 (print) ISSN 2156-5457 (online)

A cryptic new *Potamanaxas* (Hesperiidae: Pyrginae: Erynnini) stands out by terminally elongated genitalic valvae

NICK V. GRISHIN¹, DANIEL H. JANZEN² AND WINNIE HALLWACHS²

¹Howard Hughes Medical Institute and Departments of Biophysics and Biochemistry, University of Texas Southwestern Medical Center, 5323 Harry Hines Blvd, Dallas, TX, USA 75390-9050

²Department of Biology, University of Pennsylvania, Philadelphia, PA 19104

grishin@chop.swmed.edu, djanzen@sas.upenn.edu, whallwac@sas.upenn.edu

Abstract. *Potamanaxas louisghilli* Grishin, **sp. nov.** is described from Area de Conservación Guanacaste (ACG) in northwestern Costa Rica. Superficially, this species resembles several other *Potamanaxas* taxa with entire pale discal bands on the wings, but is distinguished from them by a row of faint postdiscal forewing spots (not streaks), terminally elongated genitalic valvae, and distinctive COI DNA barcodes. Found feeding on rain forest epiphytic *Cavendishia axillaris* and *Psammisia ramiflora*, the new species is likely to be host-specific to rain forest epiphytic Ericaceae, which are the food plants of all other known species of ACG *Potamanaxas* as well.

Key words: cryptic species, biodiversity, caterpillars, skipper butterflies, genitalia, Area de Conservación Guanacaste, Costa Rica.

INTRODUCTION

Potamanaxas Lindsey, 1925 (Hesperiidae: Pyrginae: Erynnini) is "a compact genus" (Evans, 1953) consisting of phylogenetically close relatives, characterized by pale discal bands on both wings, frequently disjointed into spots, and genitalic tufts of hair-like scales at the bases of the male valvae (Grishin, 2013c). After recent taxonomic changes and description of several new species (Grishin, 2013a–f), *Potamanaxas* currently includes 28 species (Warren *et al.*, 2014) and this number is likely to change upon further research. Some *Potamanaxas* species are quite rare in collections, resulting in small series of many taxa (e.g., Bell, 1956).

The species-rich specimens from a long-term comprehensive inventory of the non-leaf-miner species of Lepidoptera of Area de Conservación Guanacaste (ACG) in northwestern Costa Rica (Janzen *et al.*, 2009; Janzen & Hallwachs, 2011) are extraordinarily

Received: 20 December 2014 Accepted: 22 January 2015

Copyright: This work is licensed under the Creative Commons Attribution-NonCommercial-NoDerivs 3.0 Unported License. To view a copy of this license, visit http://creativecommons.org/ licenses/by-nc-nd/3.0/ or send a letter to Creative Commons, 171 Second Street, Suite 300, San Francisco, California, 94105, USA. useful for flushing out rarely collected species. Because most of the specimens have been reared from wild-caught caterpillars, knowledge of their traits, food plants, ecology, etc., greatly augments the usual data from adult morphology. Moreover, short sequences (ca. 658 bp) of mitochondrial DNA coding for the C-terminal segment of cytochrome c oxidase subunit 1 (COI), and dubbed "DNA barcodes", are routinely obtained for many specimens (Janzen et al., 2011), adding molecular characters to those of morphology and biology. These DNA barcodes have been remarkable flags, both indicating possible new species, and identifying recognized species (Hebert et al., 2004; Burns & Janzen, 2005; Janzen et al., 2009; 2011; 2012; Burns et al., 2008; 2010; 2013; Grishin et al., 2013a, b; 2014a, b).

Four or five *Potamanaxas* species have been found during these efforts (Janzen *et al.*, 2011; Janzen & Hallwachs, 2014). What was called *Potamanaxas unifasciata* (C. Felder & R. Felder, 1867) in earlier inventory publications is now known to be *Eburuncus unifasciata*, and is not considered here. Each ACG *Potamanaxas* brings a small puzzle to the table and requires a dedicated research project to name. One of these species, known from a series of four reared specimens, is the easiest to approach. While cryptic in wing patterns that resemble those of several other species, it differs prominently from all named taxa with entire (not separated into spots) pale bands on the forewing by having terminally elongated genitalic valvae. Here, we formally describe this species, illustrate specimens, and discuss the differences from other *Potamanaxas* taxa, both in facies and in genitalia.

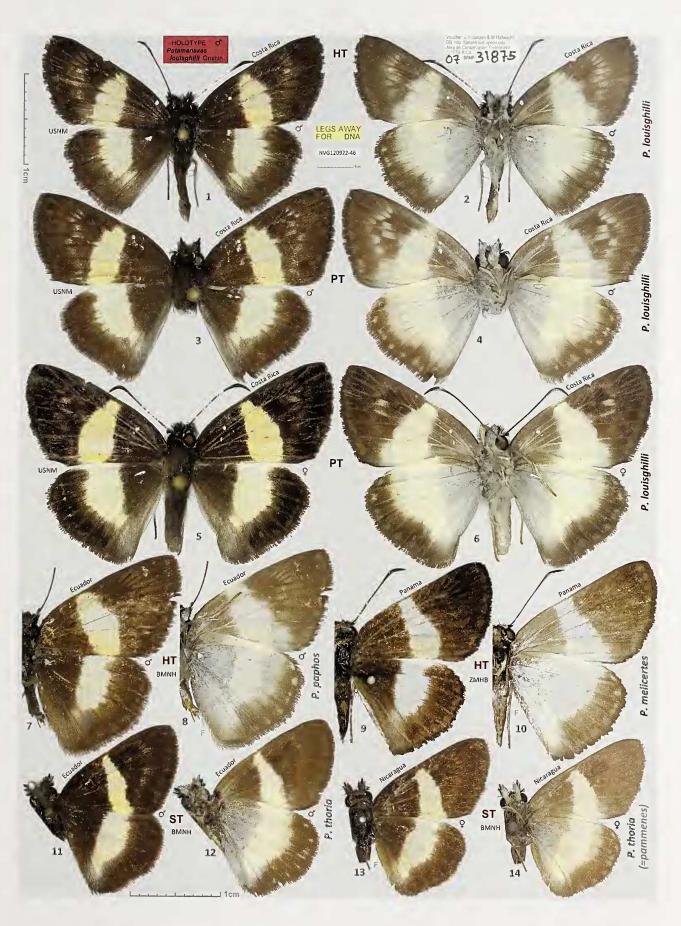
MATERIAL AND METHODS

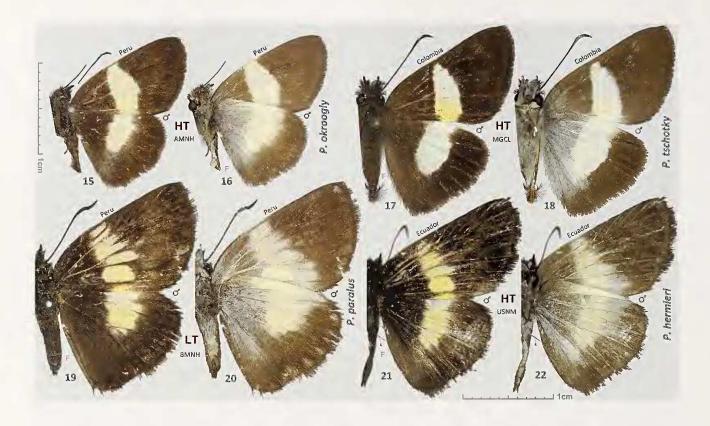
Adult specimens used in this study were from the following collections: National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM); McGuire Center for Lepidoptera and Biodiversity, Gainesville, FL, USA (MGCL); Natural History Museum, London, UK (BMNH); Museum für Naturkunde, Berlin, Germany (ZMHB); and American Museum of Natural History, New York, NY, USA (AMNH). All specimens reared from wild-caught caterpillars by the ACG inventory are so indicated by having a specimen voucher code in the format yy-SRNP-x..., where "yy" are the two last digits of a year and "x..." is the serial number of a specimen recorded in that year, from 1 to 6 digits, such as 5289 or 22467. This SRNP code can be searched for on the inventory web site (Janzen & Hallwachs, 2014) and soon, in general internet search engines. Being reared, they are different from the net-caught wild adults that usually populate museums, in that they are on average slightly smaller, owing to the food offered being of lesser quality than the food the caterpillar chooses on its own in the wild.

Standard entomological techniques were used for dissection (Robbins, 1991), i.e., the distal part of the abdomen was broken off, soaked for 40 minutes (or until cleared) in 10% KOH at 60°C (or overnight at room temperature), dissected, and subsequently stored in a small glycerol-filled vial on the pin under the specimen. Genitalia and wing venation terminology follows Steinhauser (1981). Length measurements are in metric units and were made from photographs of specimens taken next to a scale and magnified on a computer screen. Photographs of specimens and dry genitalia were taken by the author with Nikon D200 and Nikon D800 cameras through a 105 mm f/2.8G AF-S VR Micro - Nikkor lens; dissected genitalia were photographed in glycerol with the Nikon D200 camera without the lens and through microscopes at 2x, and 5x magnifications. Images were assembled and edited in Photoshop CS5.1. Genitalia photographs were taken in several focus slices and stacked in Photoshop to increase depth of field. DNA sequences were downloaded from GenBank (http://genbank.gov/) or BOLD (http://www.boldsystems.org/). They were aligned by hand (since they matched throughout their length without insertions or deletions), and analyzed using the Phylogeny.fr server (http://www.phylogeny. fr/) with default parameters (Dereeper et al., 2008). Many of these sequences have been reported in Janzen et al. (2011) and photos of specimens are available from the Area de Conservación Guanacaste (ACG) on-line database (Janzen & Hallwachs, 2014) and BOLD database (Ratnasingham & Hebert, 2007) to confirm or suggest identifications.

RESULTS AND DISCUSSION

Mass rearing of ACG caterpillars of Hesperiidae produced several species of Potamanaxas (Janzen et al., 2011), one of which clearly stands out by the morphology of its male genitalia. Terminally elongated genitalic valvae set it apart from all named Potamanaxas species with pale entire discal bands on their wings, and resemble only the genitalia of P. paralus (Godman & Salvin, 1895) and P. hermieri Grishin, 2013. However, these two species differ in having a less robust, longer tegumen relative to the uncus arms, narrower and more elongated saccus, the process of the sacculus positioned farther from the base (Fig. 24b, c), and the forewing pale band more strongly fragmented into spots (Figs. 19-22). COI DNA barcodes suggest that this ACG species might be closely related to P. paphos Evans, 1953





Figures 1–22 (continued). 15–16. *P. okroogly* holotype & Peru: Cusco Region, Quispicanchi Province, Marcapata, genitalia slide G967 [AMNH]. 17–18. *P. tschotky* holotype & Colombia: Valle del Cauca, Rio Anchicayá, elevation 1150 m, 18-Jan-1975, No. CH-473, leg. S. R. & L. M. Steinhauser, A. C. Allyn Acc. 1975-17 [MGCL]. 19–20. *P. paralus* lectotype & Peru: Cosnipata Valley, leg. H. Whitely, Godman-Salvin Collection 1912-23, type H 772, specimen No. BMNH(E) #1054005 [BMNH]. 21–22. *P. hermieri* holotype & Ecuador: Esmeraldas, km. 12.5, Lita-San Lorenzo rd., Río Chuchuví, 0° 53.01' N, 78° 30.90' W, 850 m, Jul-2002, leg. I. & R. Aldas, genitalia NVG120922-46 [USNM].

and *P. melicertes* (Godman & Salvin, 1895), which it cryptically resembles in wing pattern, but differs in prominently longer valvae and subtly in having spots vs. streaks in the forewing postdiscal pattern. This species is therefore new, and is described here.

Potamanaxas louisghilli Grishin, new species (Figs. 1-6, 23, 24a, 25)

Description: Male (n=3, Figs. 1-4) - right forewing length = 16.2 mm in holotype. Forewing twice as long as wide, rounded at apex and tornus, costa convex at the base and apex, straighter mediad, outer margin convex. Dorsal forewing dark, chocolatebrown; conspicuously pale cream-yellow (as opposed to the white on hindwing) discal band from near costa to inner wing margin, separated from costa by a narrow belt of chocolate-brown scales, narrowing towards costa; band entire, not separated into spots by veins; basal band margin typically rounded towards both wing margins; distal band margin more irregular, indented at veins; band mostly uniform in color, slightly yellower along veins; some cream scales on the costa anteriad of the band; a faint row of postdiscal pale spots (not streaks) with two spots between veins M, and M, offset distad, and a doublet of pale spots just distad of discal cell. Ventral forewing similar to dorsal in color and pattern, but overscaled with slate-colored scales at the base, discal band barely wider (mostly distad) in most cells and significantly wider

in CuA₂-1+2A cell, where rectangular slate-colored area absorbs postdiscal pale spots; band sometimes reaching costa, or separated from cream-colored costal area by very narrow line of pale brown scales; postdiscal row of pale spots (not streaks), more prominent than above, faint in some specimens, reduced and offset distad by discal cell (between veins M, and M,) and a doublet of pale spots distad of discal cell (near the bases of cells M,-M, and M,-M_s), sometimes fused with postdiscal band; row of submarginal pale-brown spots, varying from roundish to triangular, one in each cell. Hindwing nearly triangular, slightly longer than wide, rounded at apex and tornus, somewhat concave around M, and CuA, veins and convex between these veins. Dorsal hindwing dark, chocolate-brown; a mostly white discal band a quarter to a third of the wing width runs from costa to vein 2A, constricted and narrower at 1A vein, not bending towards tornus; band entire, not separated into spots by veins, margins of the band somewhat irregular, distal margin more diffuse with brown scales invading the band along the veins; white overscaling around the band near its posterior end; wing overscaled with hair-like slate-violet scales along the band towards tornus; very faint or absent submarginal paler spots in every cell. Ventral hindwing similar to dorsal, but the white band is broader distad, the wing mostly slate basad of the discal band and posteriad to anal margin, the band fused with slate area in cell 2A-3A; a row of submarginal pale-brown spots, one in each cell. Fringes brown, the same color as wing margins above and beneath everywhere, except where the pale band reaches the inner margin of forewing and costa of hindwing, and

along anal margin ventrad fringes cream-white and slate. Head and palpi chocolate-brown with small white spots above, between and behind the eyes and dispersed slate scales on palpi and collar, slate with brown scales beneath, cheeks cream, antennae brown with some slate scales at joints anteriad, a very prominent cream spot anteriad at the base of the club, spot more than half of the club length; nudum brown, of 17 segments. Thorax and abdomen chocolate-brown above, slate beneath; legs with brown, slate and cream-yellow scales, largely brown dorsally, mostly cream ventrally, forelegs with the distal half of tibia mostly white and with a prominent white ring near the distal end of tarsus (3rd and 4th tarsomeres). Male genitalia (n=2, Figs. 23, 24a) - tufts of scales near the bases of valvae orange-brown, uniformly colored; tegumen as long as wide, less than twice the length of uncus arms, with a small bulge centrally by the uncus; uncus divided, arms on the sides of tegumen, widely separated from each other, about twice as long as wide at the base; gnathos upturned and joint ventrad in the caudal half, spiculose on its surfaces caudad, widely separated from uncus: distance from gnathos ventral side to the base of uncus dorsally exceeds the length of uncus arms; saccus as long as wide, broadly triangular and broadly rounded anteriad; valva with convex costa angled in the middle, cucullus irregularly dentate along the dorsal edge, extending caudad for about the same length as costa, cucullus caudal end narrow, rounded and directed posterodorsad, at the base of dorsal margin cucullus with a triangular tooth-like projection directed anterodorsad, dorsolateral dimension of the valva ("height") is about the cucullus length; sacculus with style-like projection from its very base, projection about twice as long as wide, not widening dorsad; penis slightly shorter than valva length, no cornuti.

Female (n=1, Figs. 3, 4) – right forewing length = 17.4 mm, similar to male but slightly larger, nudum of 17 segments. *Female genitalia* (Fig. 25) – lamella postvaginalis with two approximately triangular sclerotized areas along the distal margin with a non-sclerotized break between them in the middle; lamella antevaginalis weakly sclerotized, expanded anteriad with several stronger sclerotized latitudinal ridges; antrum poorly sclerotized, not prominent, narrow; ductus bursae narrow, slightly longer than sterigma; corpus bursae longer that the rest of genitalia, as wide as sterigma.

Barcode sequence of the holotype: Genbank Accession JF762690, voucher 07-SRNP-31875, 658 base pairs:

AACTTTATATTTTATCTTTGGAATTTGAGCAGGAATAGTAGGAACT TCCCTAAGTTTATTATTCGAACTGAATTAGGTAATCCAGGATCAT TAATTGGGGATGATCAAATTTATAATACTATTGTTACAGCTCAT GCTTTTATTATAATTTTTTTTATAGTTATACCAATTATAATTGAG GATTTGGTAATTGATTAGTGCCATTAATACTAGGAGCCCCAGA TATAGCATTTCCTCGAATAAATAATAATAATAAGATTTTGACTTTTAC CCCCCTCTTTAATATTATTAATTTCTAGAAGAATCGTAGAAAATG GAGCAGGAACAGGTTGAACTGTTTACCCCCCCTTATCTGCCAAT ATTGCTCACCAAGGTTCCTCAGTAGATTTAGCTATTTTCTCCCT TCATTTAGCAGGTATTTCTTCTAGCAATTAGCTATTTATC CACAACAATTATTAATATCAGAATTAGGAATTATTAT CACAACAATTATTAATATCGAATTAGGAATTACTGCTTTACTAT TACTACTTTCATTATTAATATCGAGTGCGAATTACTGCTTTACTAT TACTACTTTCATTACCTGTATTAGCAGGTGCTATTACTATTAT TAACAGAATCGAAATTTAAATACAACCTTTTTTGACCCAGCAGGAG GAGGAGATCCAATTTTAATTACAACATTTATT

Sequences of paratypes show differences in 2 positions.

Types: *Holotype* ♂ (Figs. 1, 2, 23a–c) has the following four rectangular labels: white printed & hand-printed - || Voucher: D.H.Janzen & W.Hallwachs | DB: http://janzen.sas.upenn.edu | Area de Conservacion Guanacaste, | COSTA RICA. | 07-SRNP-31875 ||; yellow printed - || LEGS AWAY | FOR DNA ||; white printed - || NVG120922-46 ||; red printed - || HOLOTYPE ♂ | *Potamanaxas | louisghilli*Grishin ||. Holotype data: Costa Rica: Area de Conservación Guanacaste, Guanacaste Province, Sector Pitilla, site Sendero

Memos, 10.98171° -85.42785°, 740 m, collected on 29-Mar-2007 in antepenultimate instar feeding on Cavendishia axillaris (Ericaceae) by Lucia Ríos, eclosed 2-May-2007, voucher code 07-SRNP-31875, genitalia NVG120922-46, Genbank accession of barcode sequence JF762690. Paratypes: Costa Rica: Area de Conservación Guanacaste, Guanacaste Province, Sector Pitilla: 1 & (Figs. 3, 4, 23d-j) site Estacion Pitilla, 10.98931° -85.42581°, 675 m, collected on 12-Mar-1991 in ultimate instar feeding on Cavendishia axillaris (Ericaceae), eclosed 7-Apr-1991, voucher code 91-SRNP-132, genitalia No. X-6125 J. M. Burns 2005, Genbank accession of barcode sequence DQ293099; 1 3, site Orosilito, 10.98332° -84.43623°, 900 m, collected on 12-Apr-2014 in penultimate instar feeding on Psammisia ramiflora (Ericaceae) by Manel Rios, eclosed 25-Apr-2014, voucher code 14-SRNP-30571; 1 ♀ (Figs. 5, 6, 24) site Sendero Memos, 10.98171° -85.42785°, 740 m, collected on 16-Apr-2011 in penultimate instar feeding on Cavendishia axillaris (Ericaceae) by Freddy Quesada, eclosed 13-May-2011, voucher code 11-SRNP-31012, genitalia NVG131102-92, Genbank accession of barcode sequence JQ526704.

Deposition of types: The holotype and the three paratypes are in the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM).

Type locality: COSTA RICA: Area de Conservación Guanacaste, Guanacaste Province, Sector Pitilla, site Sendero Memos, GPS: 10.98171° –85.42785°, elevation 740 m.

Etymology: This species is named in memory of Louis G. Hill, a deeply principled Pennsylvania State Senator and Philadelphia Judge and lover of wilderness, whose children are supporters of ACG and the dissemination of ACG insect knowledge, and particularly the taxonomy of the subfamily Campopleginae in the parasitoid wasp family Ichneumonidae, many of which are parasitoids of skipper butterfly (Hesperiidae) caterpillars.

Distribution and phenology: Currently, this species is known only from about 10 km² of ACG mid-elevation Caribbean rain forest (but geopolitically in Guanacaste Province, which is largely dry forest), but it is expected to have a wider distribution throughout Costa Rica and Panama. Specimens with similar genitalia have been recorded from South America as well, and the research on their taxonomic status is on-going. The caterpillars were found in March-April and the adults eclosed in April-May (Janzen & Hallwachs, 2014).

Diagnosis: This species belongs to Potamanaxas because it has all the traits of the genus as given in the Evans identification key (1953: 6-15, 137). In particular, males have two tufts of hair-like scales near the bases of valvae (Fig. 23e, f), a suggested synapomorphy of Potamanaxas (Grishin, 2013a; 2013b; 2013d). By the COI barcodes, it nests within other Potamanaxas species (Ratnasingham & Hebert, 2007; Janzen et al., 2011). As suggested by COI barcodes and wing patterns, the new species is most similar to P. paphos Evans, 1953 and P. melicertes (Godman & Salvin, 1895) (Figs. 7-10), but is confidently distinguished from them by terminally elongated valvae (Figs. 23, 24). P. louisghilli could also be confused with other Potamanaxas species characterized by pale discal bands on wings, such as P. thoria (Hewitson, 1870) (Figs. 11-14, 24d), P. okroogly Grishin, 2013 (Figs. 15, 16, 24e), P. tschotky Grishin, 2013 (Figs. 17, 18, 24g), P. paralus (Godman & Salvin, 1895) (Figs. 19, 20, 24b), and P. hermieri Grishin, 2013 (Figs. 21, 22, 24c), but can be distinguished from these species either by wing patterns or male genitalia (Figs. 23, 24).

A combination of the following characters is diagnostic of *P. louisghilli*: (1) The yellowish cream—not strong yellow as in *P. flavofasciata* (Hewitson, 1870) and *P. xantholeuce* (Mabille, 1888)—discal band on dorsal forewing is entire and not separated into spots by veins as in most *Potamanaxas* species (see Warren et al. 2014 for illustrations); its margins could be somewhat irregular (e.g., Fig. 1), but not as irregular as in *P. paralus* (Fig. 19), *P. hermieri* (Fig. 21), and *P. xantholeuce*. (2) The pale-cream-white discal band on dorsal hindwing spans from the costa to the 2A vein and has irregular margins, not sharply defined as in *P. okroogly* (Fig. 15) and

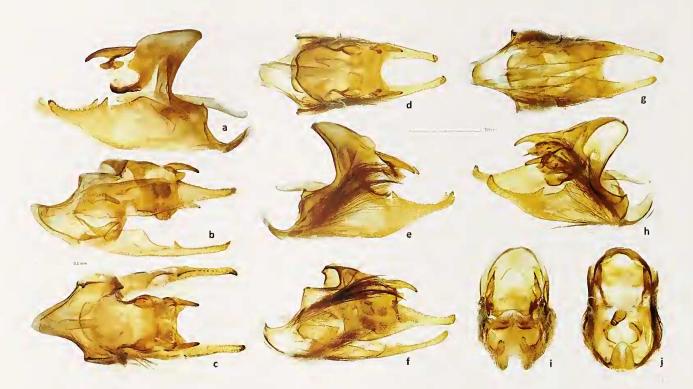


Figure 23. Male genitalia of *Potamanaxas louisghilli* n. sp. Genital capsule of the holotype (a–c, voucher 07-SRNP-31875, genitalia NVG120922-46, Figs. 1–2) and a paratype (d–j, voucher 91-SRNP-132, genitalia No. X-6125 J. M. Burns 2005, Figs. 3–4) in different views: a, e. lateral; b, f. left ventrolateral; c, d. dorsal; g. ventral; h. right dorsolateral; i. posterior; j. anterior. Specimens are in USNM.

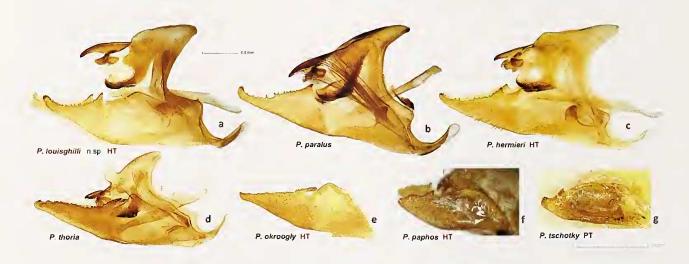


Figure 24. Male genitalia of *Potamanaxas.* **a.** *P. louisghilli* holotype, data in text (Figs. 1–2); **b.** *P. paralus*, Peru: Huánuco Region, Tingo María, 23-Jun-1982, 800 m, genitalia #H747 by S. S. Nicolay [USNM]; **c.** *P. hermieri* holotype, Ecuador: Esmeraldas, km. 12.5, Lita-San Lorenzo rd., Río Chuchuví, 0° 53.01' N, 78° 30.90' W, 850 m, Jul-2002, leg. I. & R. Aldas, genitalia NVG120922-46 [USNM] (Figs. 21–22); **d.** *P. thoria*, Ecuador: Imbabura Prov., Ruminahui, 37 km N. Pedro Vicente Maldonado, 0° 16.73'N 78° 59.9'W, 500 m, 9-Mar-2001, leg. D. H. Ahrenholz, genitalia NVG120922-44 [USNM], lateral view; **e.** *P. okroogly* holotype, Peru: Cusco Region, Quispicanchi Province, Marcapata, genitalia slide G967 [AMNH], left valva, interior view (Figs. 15–16); **f.** *P. paphos* [holo]type, Ecuador: Paramba, dry season, Apr-1897, 3500', leg. Rosenberg, Rothschild Bequest B.M. 1939-1, specimen No. BMNH(E) #1054150 [BMNH], lateral view of the abdomen caudal end (Figs. 7–8); **g.** *P. tschotky* paratype, Ecuador, coll. Saunders, Godman-Salvin collection 1912–23, specimen No. BMNH(E) #1054120 [BMNH], left valva, interior view. "F" indicates mirror image (left-right inverted). Images of BMNH specimens are copyright of Trustees of the Natural History Museum, London; used with permission.



Figure 25. Female genitalia of *Potamanaxas louisghilli* n. sp. a. complete genitalia in ventral view with a scale bar on the left; b-d magnified sterigma, ovipositor lobes, and last tergum in posteroventral (b), ventral (c) and right lateroventral (d) views, scale bar on the right. Voucher 11-SRNP-31012, genitalia NVG131102-92, Figs. 5–6, the specimen is in USNM.

P. tschotky (Fig. 17); the band does not end posterior to discal cell near CuA, vein as in P. hirta (Weeks, 1901), P. okroogly (Fig. 15), P. tschotky (Fig. 17), and P. effusa (Draudt, 1922), and does not bend towards the tornus as in P. thoria (Fig. 11); the posterior end of the band is partly separated from the rest of the band by a constriction along the 1A vein (Figs. 1, 3, 5) and the inner margin of the band is indented at the 1A vein, not smooth as in P. thoria (Fig. 11). (3) A row of faint postdiscal forewing spots, not streaks as in P. paphos and P. melicertes (Figs. 7-10), is complemented with a doublet of spots distad of discal cell; the spots can be seen above (Figs. 1, 3, 5), but are more prominent beneath (Figs. 2, 4, 6); the spots are typically more expressed and elongated than those in P. thoria (Figs. 11-14); two spots of the row, those between cells M, and M_s, are offset distad, making room for an additional spot doublet just distad of discal cell (at the bases of cells M1-M2 and M2-M2), this doublet is usually made of the best-developed spots (Fig. 6). (4) Males have a white streak at the front of antennal club and a white ring on foreleg tarsi, as in P. tschotky (Grishin 2013d); those are normally absent in other related species, except for the antennal streak in P. thoria and P. okroogly. (5) Male genitalic valvae are characterized by an elongated and curved dorsad cucullus with a tooth at its base directed anterodorsad (Fig. 23a, e, most similar to P. paralus and P. hermieri, but different in most other Potamanaxas species), and the process on the sacculus stemming from its very base (positioned further posteriad in P. paralus Fig. 24b and P. hermieri Fig. 24c); the saccus is rather broad, almost triangular with a broadly rounded apex (narrower in P. paralus and P. hermieri); and the tegumen is more robust and relatively shorter compared to uncus arms than in P. paralus and P. hermieri.

Characters (1) to (3) are usually sufficient to identify *P. louisghilli* from specimens, live individuals, and their photographs, making dissection unnecessary. However, the structure of male genitalia and its differences from other *Potamanaxas* species are instrumental in substantiating *P. louisghilli* as a species-level taxon and its distinctness from cryptically similar *P. paphos* and *P. melicertes*. Additionally, *P. louisghilli* is clearly different by its DNA barcode from the other recorded species of ACG *Potamanaxas*.

Immatures and foodplants: Caterpillars that produced all specimens in the type series were found feeding on *Cavendishia axillaris* and *Psammisia ramiflora*, both in Ericaceae. It is likely to be host-specific to rain forest epiphytic Ericaceae, as are the other species of ACG *Potamanaxas* (Janzen *et al.*, 2011).

ACKNOWLEDGEMENTS

We are indebted to the ACG parataxonomists for finding and rearing the caterpillars; to ACG for taking care of them and their caterpillars; to the Biodiversity Institute of Ontario at the University of Guelph, Canada, as well as BOLD of iBOL (http://www.boldsystems. org/) for sequencing and analyzing the DNA barcodes. We are grateful to Robert K. Robbins, John M. Burns and Brian Harris (National Museum of Natural History, Smithsonian Institution, Washington DC), David Lees and Blanca Huertas (Natural History Museum, London, UK), Andrew D. Warren and Andrei Sourakov (McGuire Center for Lepidoptera and Biodiversity, Gainesville, FL), Wolfram Mey (Museum für Naturkunde, Berlin, Germany), Andrew Johnston, David A. Grimaldi and Suzanne Rab Green (American Museum of Natural History, New York, NY) for facilitating access to the collections under their care and stimulating discussions; to Don Harvey (National Museum of Natural History, Smithsonian Institution, Washington DC) for preparations of genitalia from the John Burns X-series; to Bernard Hermier for many enlightening discussions, and numerous suggestions; and anonymous reviewers for helpful comments. The study has been supported (DHJ and WH) by U.S. National Science Foundation grants BSR 9024770 and DEB 9306296, 9400829, 9705072, 0072730, 0515699, and grants from the Wege Foundation, International Conservation Fund of Canada, Jessie B. Cox Charitable Trust, Blue Moon Fund, Guanacaste Dry Forest Conservation Fund, Area de Conservación Guanacaste, Permian Global, JRS Biodiversity Foundation, USNM/Smithsonian and the University of Pennsylvania.

EDITOR'S NOTE

The electronic edition of this article has been registered in ZooBank to comply with the requirements of the amended International Code of Zoological Nomenclature (ICZN). This registration makes this work available from its electronic edition. ZooBank is the official registry of Zoological Nomenclature according to the ICZN and works with Life Science Identifiers (LSIDs). The LSID for this article is: urn:lsid:zoobank. org:pub:82159950-B38C-42F4-BACE-8694C1AEA4C7. Registration date: May 2nd, 2015. This record can be viewed using any standard web browser by clicking on the LSID above.

LITERATURE CITED

- BELL, E. L. 1956. Descriptions of some new species of Neotropical Hesperiidae (Lepidoptera, Rhopalocera). American Museum Novitates 1778: 1–13.
- BURNS, J. M. & D. H. JANZEN. 2005. Pan-Neotropical genus Venada (Hesperiidae: Pyrginae) is not monotypic: Four new species occur on one volcano in the Area de Conservación Guanacaste, Costa Rica. Journal of the Lepidopterists' Society 59(1): 19-34.
- BURNS, J.M., D.H. JANZEN, M. HAJIBABAEI, W. HALLWACHS & P.D.N. HEBERT. 2008. DNA barcodes and cryptic species of skipper butterflies in the genus *Perichares* in Area de Conservación Guanacaste, Costa Rica. Proceedings of the National Academy of Sciences 105(17): 6350–6355.
- BURNS, J. M., D. H. JANZEN & W. HALLWACHS. 2010. Of many similar species in the Neotropical genus *Porphymogenes* (Lepidoptera: Hesperiidae), a new one, repeatedly reared in Costa Rica, is relatively distinct. Proceedings of the entomological Society of Washington 112(1): 32–42.
- BURNS, J. M., D. H. JANZEN, W. HALLWACHS & M. HAJIBABAEI. 2013. DNA barcodes reveal yet another new species of *Venada* (Lepidoptera: Hesperiidae) in northwestern Costa Rica. Proceedings of the Entomological Society of Washington 115(1): 37–47.
- EVANS, W. H. 1953. A catalogue of the American Hesperiidae indicating the classification and nomenclature adopted in the British Museum (Natural History). Part III (Groups E, F, G) Pyrginae. Section 2. London, British Museum (Natural History). v + 246 pp., pls. 26–53.
- GRISHIN, N. V. 2013a. Uncus shaped akin to elephant tusks defines a new genus for two very different-in-appearance Neotropical skippers (Hesperiidae: Pyrginae). Journal of Research on the Lepidoptera 45: 101–112.
- GRISHIN, N. V. 2013b. On the identity of *Potamanaxas andraemon* and its relatives, with the description of a new species from Peru (Hesperiidae: Pyrginae: Erynnini). Tropical Lepidoptera Research 23(1): 1–13.
- GRISHIN, N. V. 2013c. Adding to the rich fauna of the Chocó region in Ecuador, a newspecies of *Potamanaxas* (Hesperiidae: Pyrginae: Erynnini). Tropical Lepidoptera Research 23(2) (Suppl. 1): 1–5, pls 1-3.
- GRISHIN, N. V. 2013d. A new Potamanaxas (Hesperiidae: Pyrginae: Erynnini), patterned like *P. bana*, but with sickle-armed genitalia, not chicken claws. Tropical Lepidoptera Research 23(2) (Suppl. 1): 6–9, pls 4-6.
- GRISHIN, N. V. 2013e. An enigmatic new Potamanaxas (Hesperiidae: Pyrginae: Erynnini) is a visual mosaic of characters from distantly related species. Tropical Lepidoptera Research 23(2) (Suppl. 1): 10–12, pls 8-10.
- GRISHIN, N. V. 2013f. Two new species of *Potamanaxas* (Hesperiidae: Pyrginae: Erynnini)—one of them, *P. melicertes* of Evans, was mentioned but not named by Godman and Salvin. Tropical Lepidoptera Research 23(2) (Suppl. 1): 13–17, pls 11-14.
- GRISHIN, N.V., J. M. BURNS, D. H. JANZEN, W. HALLWACHS & M. HAJIBABAEL 2013a. Oxynetra: facies and DNA barcodes point to a new species from Costa Rica (Hesperiidae: Pyrginae: Pyrrhopygini). Journal of the Lepidopterists' Society 67(1): 1–14.

- GRISHIN, N. V., D. H. JANZEN & W. HALLWACHS. 2013b. Hiding behind gaudy looks, a new Central American species of *Phareas* (Hesperiidae: Eudaminae). Journal of the Lepidopterists' Society 67(3): 161–174.
- GRISHIN, N. V., D. H. JANZEN & W. HALLWACHS. 2014a. A new species of *Eracon* (Hesperiidae: Pyrginae) substantiated by a number of traits, including female genitalia. Journal of the Lepidopterists' Society 68(3): 149–161.
- GRISHIN, N. V., J. M. BURNS, E. BROCKMANN, W. HALLWACHS & D. H. JANZEN. 2014b. A cryptic new *Jemadia* (Hesperiidae: Pyrginae: Pyrrhopygini) from Costa Rica and Panama with a subtly distinctive combination of blue rays and white bands. Journal of the Lepidopterists' Society 68(4): 232–247.
- HEBERT, P.D. N., E. H. PENTON, J. M. BURNS, D. H. JANZEN & W. HALLWACHS. 2004. Ten species in one: DNA barcoding reveals cryptic species in the neotropical skipper butterfly *Astraptes fulgerator*. Proceedings of the national Academy of Sciences of the USA 101(41): 14812–14817.
- JANZEN, D. H. & W. HALLWACHS. 2011. Joining inventory by parataxonomists with DNA barcoding of a large complex tropical conserved wildland in northwestern Costa Rica. PLoS ONE 6(8): e18123.
- JANZEN, D. H. & W. HALLWACHS. 2014. Dynamic database for an inventory of the macrocaterpillar fauna, and its food plants and parasitoids, of Area de Conservación Guanacaste (ACG), northwestern Costa Rica. http://janzen.sas.upenn.edu/>.
- JANZEN, D. H., W. HALLWACHS, P. BLANDIN, J. M. BURNS, J.-M. CADIOU, I. A. CHACÓN, T. DAPKEY, A. R. DEANS, M. E. EPSTEIN, B. ESPINOZA, J. G. FRANCLEMONT, W. A. HABER, M. HAJIBABAEI, J. P. W. HALL, P. D. N. HEBERT, I. D. GAULD, D. J. HARVEY, A. HAUSMANN, I. KITCHING, J. D. LAFONTAINE, J.-F. LANDRY, C. LEMAIRE, J. Y. MILLER, J. S. MILLER, L. D. MILLER, S. E. MILLER, J. J. MONTERO, E. G. MUNROE, S. RAB GREEN, S. RATNASINCHAM, J. E. RAWLINS, R. K. ROBBINS, J. J. RODRIGUEZ, R. ROUGERIE, M. J. SHARKEY, M. A. SMITH, M. A. SOLIS, J. B. SULLIVAN, P. THIAUCOURT, D. B. WAHL, S. J. WELLER, J. B. WHITFIELD, K. R. WILLMOTT, D. M. WOOD, N. E. WOODLEY & J. J. WILSON. 2009. Integration of DNA barcoding into an ongoing inventory of complex tropical biodiversity. Molecular Ecology Resources 9 (Supplement 1): 1–26.
- JANZEN D. H., W. HALLWACHS, J. M. BURNS, M. HAJIBABAEI, C. BERTRAND & P. D. N. HEBERT. 2011. Reading the complex skipper butterfly fauna of one tropical place. PLoS ONE 6(8): e19874.
- JANZEN, D. H., W. HALLWACHS, D. J. HARVEY, K. DARROW, R. ROUGERIE, M. HAJIBABAEI, M. A. SMITH, C. BERTRAND, I. C. GAMBOA, B. ESPINOZA, J. B. SULLIVAN, T. DECAENS, D. HERBIN, L. F. CHAVARRIA, R. FRANCO, H. CAMBRONERO, S. RIOS, FR. QUESADA, G. PEREIRA, J. VARGAS, A. GUADAMUZ, R. ESPINOZA, J. HERNANDEZ, L. RIOS, ELIETH CANTILLANO, ROSTER MORAGA, CALIXTO MORAGA, PETRONA RIOS, MANUEL RIOS, RICARDO CALERO, D. MARTINEZ, D. BRICEÑO, M. CARMONA, E. AFU, K. ARAGON, C. UMAÑA, J. PEREZ, A. CORDOBA, P. UMAÑA, G. SIHEZAR, O. ESPINOZA, C. CANO, E. ARAYA, D. GARCIA, H. RAMIREZ, M. PEREIRA, J. CORTEZ, M. PEREIRA, W. MEDINA & P. D. N. HEBERT. 2012. What happens to the traditional taxonomy when a well-known tropical saturniid moth fauna is DNA barcoded? Invertebrate Systematics 26:478–505.
- RATNASINGHAM, S. & P. D. N. HEBERT. 2007. BOLD : The Barcode of Life Data System (www.barcodinglife.org). Molecular Ecology Notes 7, 355–364.
- ROBBINS, R. K. 1991. Evolution, comparative morphology, and identification of the Eumaeine butterfly genus *Rekoa* Kaye (Lycaenidae: Theclinae). Smithsonian Contributions to Zoology 498:1–64 pp.
- SELANDER, R. B. & P. VAURIE. 1962. A gazetteer to accompany the "Insecta" volumes of the "Biologia Centrali-Americana". American Museum Novitates 2099: 1–70.
- STEINHAUSER, S. R. 1981. A revision of the *proteus* group of the genus *Urbanus* Hübner. Lepidoptera: Hesperiidae. Bulletin of the Allyn Museum 62: 1–41.
- WARREN, A. D., K. J. DAVIS, E. M. STANGELAND, J. P. PELHAM & N. V. GRISHIN. 2014. Illustrated lists of American butterflies. [28-JX-2014] http://www.butterfliesofamerica.com>.